J. Ethnobiol. 15(1):119–148 Summer 1995

PREHISTORIC CERAMIC AGE ADAPTATION TO VARYING DIVERSITY OF ANIMAL RESOURCES ALONG THE WEST INDIAN ARCHIPELAGO

ELIZABETH S. WING
Florida Museum of Natural History
Gainesville, FL 32611
and
STEPHEN R. WING
Division of Environmental Studies
University of California
Davis, CA 95616

ABSTRACT.—We apply island biogeographic principles to the analysis of archaeological faunas from Caribbean Ceramic age sites, and use the results to better understand human adaptations to these island settings. Faunal samples from groups of islands, the Lesser Antilles, Greater Antilles and Virgin Islands, Bahamas, and Turks and Caicos, share characteristics and can be analyzed in these island groups as well as individually. Despite variation within these island groups, they reflect decreased diversity with distance from the mainland and a positive correlation between diversity and island size. Though the colonists were subject to the limitations described by island biogeographic principles, they were also able to exert some control by disproportionately enriching the diversity of species on small islands by introducing animals.

RÉSUMÉ.—Nous appliquons des principes bio-géographiques insulaires à l'analyse des faunes archéologique des sites caraïbes de la période céramique. Nous utilisons les résultats pour mieux comprendre les adaptations humaines à ces environnements insulaires. Des échantillons de faune de groupes d'îles, Les Petites Antilles, les Grandes Antilles avec les Iles Vièrges, et les Bahamas, les Turques et les Caïcos, ont des caractéristiques communes et forment trois groupes. Malgré une certaine variation à l'intérieur de ces groupes, ils reflétent une diversité décroissante en fonction de la distance du continent et une corrélation positive entre la diversité et les dimensions de l'île. Bien que les colons furent subordonnés à des limitations inscrites par les principes bio-géographiques insulaires, ils étaient aussi capables, en introduisant des animaux, d'exercer une influence sur l'enrichissement disproportionné de la diversité des espèces des petites îles.

RESUMEN.—Aplicamos principios de la biogeografíca de islas al análisis de faunas arqueológicas de sitios de la era cerámica en el Caribe, y empleamos los resultados para entender mejor las adaptaciones humanas a estos escenarios isleños. Las muestras de fauna de grupos de islas, las Antillas Menores, las Antillas Mayores y las Islas Vígenes, y las Bahamas, Turcos y Caicos, comparten características y pueden ser analizadas en estas agrupaciones de islas, así como en forma individual. A pesar de la variación dentro de estos grupos de islas, reflejan una disminución de la diversidad a mayor distancia de la tierra firme, y una correlación positiva entre diversidad y tamaño de la isla. Si bien los colonizadores estuvieron sujetos a las limitaciones descritas por los principios biogeográficos de islas, pudieron también ejercer cierto control al enriquecer desproporcionalmente la diversidad de especies en islas pequeñas mediante la introducción de animales.

INTRODUCTION

Native American colonization of the West Indian archipelago was fraught with uncertainties. These early colonists faced distant ocean voyages to islands with unfamiliar plants and animals. They did not know whether they would find resources they were accustomed to using in sufficient quantities to sustain life. All of the resources they required for food, medicine, and the raw materials for construction of tools, equipment, shelter, and clothing had to be met by the plants and animals of the island, its surrounding waters, and whatever was imported. The animals that were used for food and whose remains were incorporated in archaeological deposits are evidence for the ways the colonists coped with the differences they found in island faunas.

Despite the uncertainties Native Americans faced, they did colonize the West Indies, Bahamas, and the Turks and Caicos islands (Fig. 1). Whether they were pushed by population pressures on the mainland or were drawn by the potentials of the islands is still debated. Whatever the force that initiated migration, Amerindians moved into the West Indies from at least two fronts and came in at least three waves of migration (Rouse 1992). The first wave of migration took place around 4000 B.C. and originated in Middle America. These people with Casamiroid culture settled in western Cuba. The second and subsequent waves of migration originated from the northeastern coast of South America. The second migration occurred around 2000 B.C. bringing people with Ortoiroid culture into the Lesser Antilles and the Virgin Islands. The third and largest wave of migration began about 250 B.C. These people, belonging to the Ceramic age, colonized virtually all of the islands of the West Indies and the Bahamas by the time Europeans explored the Caribbean. The adaptation of these Ceramic age people to the island ecosystem is the focus of this paper. The data upon which it is based are samples of animal remains excavated from this third period of settlement.

A better understanding of the kinds and diversity of plants and animals that might be found on islands such as the West Indies is provided by research stimulated by the seminal work on island biogeography by MacArthur and Wilson (1967). The equilibrium theory that stems from this research considers the numbers of species occurring on islands to be the dynamic balance between immigration and extinction (Connor and McCoy 1979:806). As a consequence, the diversity of species on islands decreases with the distance of the island to the mainland source of species (MacArthur and Wilson 1967). Thus, human colonists would encounter ever fewer species the further they ventured from the mainland. The number of species on an island is also related to the area of the island. This relationship, known as the species-area curve, is best described by the power function model, log species/log area. People settling on smaller islands would theoretically find fewer species than those settling on larger islands at equal distance from a source of species. Many studies of the species/area curves of different organisms have found that the slopes of these curves fall within the

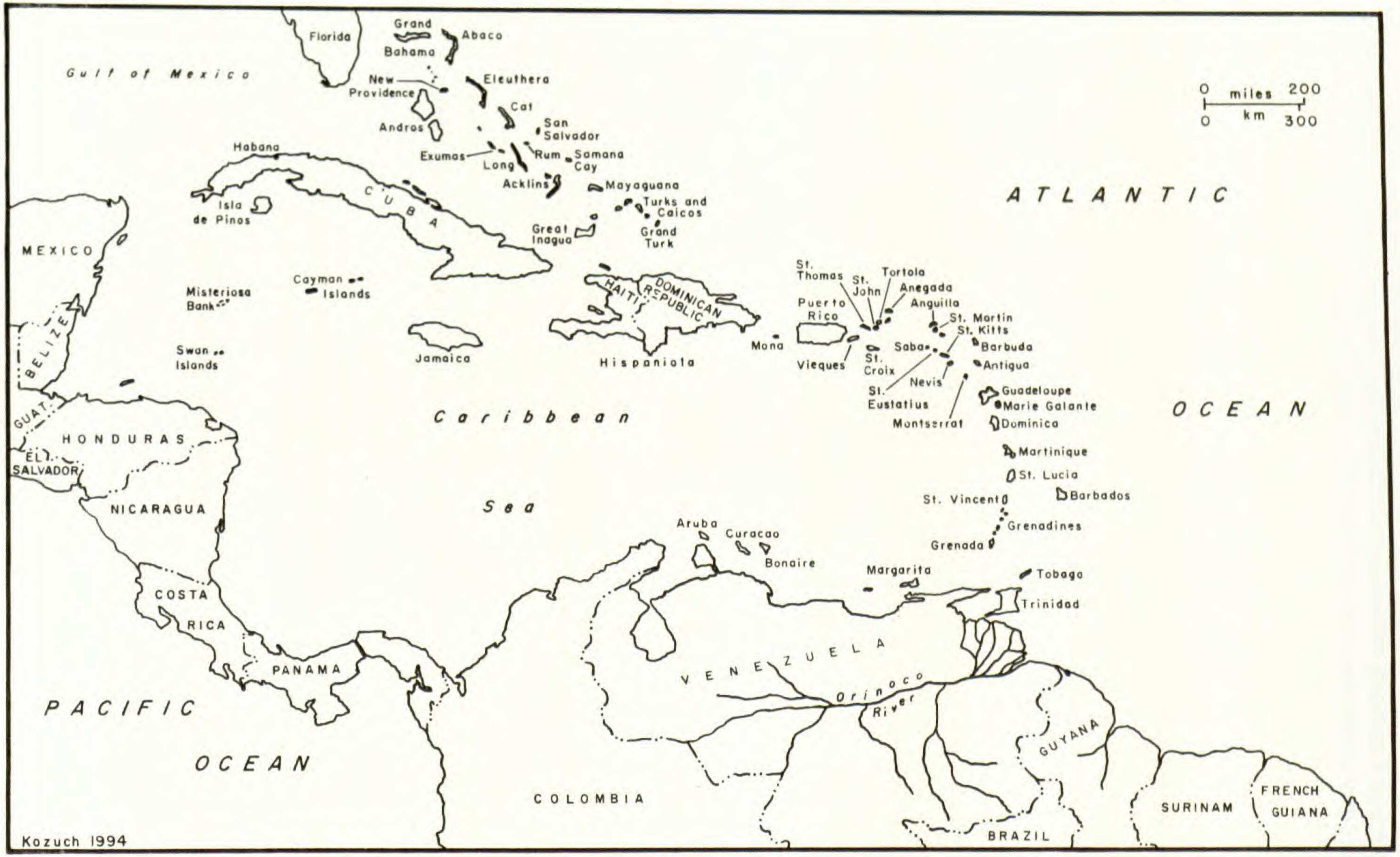


FIG. 1.—Map of the West Indies.

range of 0.20 to 0.40 (Connor and McCoy 1979:801). We use this range to evaluate the effects on human exploitation of the decreased diversity of animal resources found on small isolated islands.

Our focus is to apply island biogeographic principles to the analysis of archaeological faunas, and use the results to gain a better understanding of human adaptations to these island settings. Ideally, we would compare the archaeological faunas directly with the modern faunas of the islands. However, introductions of both New and Old World animals, extinctions of endemic species, and landscape modifications for plantation agriculture have so drastically modified the island faunas, as they were found by Amerindians, that direct comparisons are no longer appropriate (Woods 1989, 1990). Instead, we assess an array of faunal assemblages from the perspective of general biogeographic principles derived from many studies of the distribution of plants and animals (Preston 1962; Hamilton et al. 1964; MacArthur and Wilson 1967; Connor and McCoy 1979; Woods 1990). We use individual abundance, generic richness as seen in the slopes of log species/log area curves, diversity and equitability, and similarity indices for this analysis of a series of vertebrate faunal assemblages excavated from archaeological sites in the Caribbean (Table 1). We also divide the faunal samples into habitat specific subsamples and extend our analysis to include the relative contributions of each to the fauna as a whole. The resulting patterns provide a better understanding of the nature of human adaptation to colonization of the West Indian island archipelago.

MATERIALS AND METHODS

Site selection.—We follow three guidelines in the choice of sites for this study. The sites are chosen to represent past resource exploitation throughout the West Indies and as such are located in a broad array along the island chain. Only samples recovered using a fine gauge screen sieving strategy are included in this study. The samples come from midden refuse and, whenever possible, from deposits that accumulated during the early ceramic period. Our choice of archaeological faunal samples are intended to insure both the greatest comparability of recovery methods and archaeological context as well as the widest geographic distribution of the samples.

The faunal samples come from 18 sites located on 13 islands, six in the Lesser Antilles, two in the Virgin Islands, two in the Greater Antilles, and three in the Bahamas, Turks and Caicos (Table 1; Fig. 1). The majority, 16, of the sites are located directly on the coast. Two sites, Hope Estate on St. Martin and Tutu on St. Thomas, are in the higher elevation, interior of these islands, 2 km from the shore.

The samples are all from Ceramic age contexts deposited by people who practiced agriculture (Newsom 1993). The matrix of these deposits is composed of mollusc and crab shell. Three of the samples are features, features 4 and 25 from En Bas Saline and feature 104 from Maisabel. All samples are identified by the excavators as midden refuse. The animal remains in them represent primarily food remains. The vertebrate remains are primarily small- and medium-sized individuals weighing from 100 to 500 gr. Some of their fragmentary remains are

TABLE 1.—The faunal samples analyzed. Their island location, dates of the deposits, and reference are presented. C^{14} dates are listed as the mean and standard deviation BP and the number of the issuing laboratory. In the absence of C^{14} dates, chronological dates spanning the years of the production of dated pottery associated with the faunal remains are given.

Island	Site Name	Date	Reference
Bahamas			
1. Samana Cay	SM-2, SM-7	AD 1000–1500	Watford[1], Hoffman[1]
2. Crooked Is.	CR-8, CR-14	AD 1000–1500	deFrance 1991
Turks and Caicos			
3. Middle Caicos	MC-6, MC-12	AD 750–1500	Wing and Scudder 1983
Greater Antilles			
4. Hispaniola	En Bas Saline (fea. 4 and 25)	AD 1250–1500	Deagan 1988
5. Puerto Rico	Maisabel	AD 200–600	deFrance 1988
Virgin Islands			
6. St. John	Trunk Bay	AD 100–800	Wild[1]
	Calabash Boom	AD 1050 ± 60	Caesar[1]
7. St. Thomas	Tutu (2044 lv.D&F)	1430 ± 90 BP (Beta 62568)	Wing et al. 1993
Lesser Antilles			
8. St, Martin	Hope Estate	2250 ± 45 BP (PITT-0220)	Haviser 1988
9. Saba	Kelbey's Ridge	AD 670–1350	Hofman 1993
	Spring Bay (unit 31)	655 ± 30 BP (GrN -16773)	Hofman 1993
10. Nevis	Hichman's (GE-5)	AD 0–600	Wilson[1]
	Indian Castle (GE-1)	1280 ± 60 BP (Beta-19327)	Wilson[1]
11. Antigua	Mill Reef	AD 500–1150	Wing et al. 1968
12. Barbados	Silver Sands	650 ± 100 BP (I-16,215), 990 ± 80 BP (I-16,215)	Drewett 1991
13. Grenada	Pearls	AD 200	Fandrich 1990, Stokes 1991

[1] personal communication

burned. Associated with the food remains may be the remains of intrusive animals such as the small land snails found in most sites.

Excluded from analysis are contexts with burials. Dogs are usually found with many associated parts of the skeleton and often recovered in association with human burials in the West Indies (Wing 1991). A burial of an agouti, *Dasyprocta* sp., was recovered from the Sugar Factory Pier site on St. Kitts (Goodwin 1975 letter). These burials are of animals that are either known to be domestic or tame and managed. By excluding burials from analysis, we lean on the side of caution to not overstate a case for the practice of manipulating the faunal resources of the islands. It is possible that other animals that had special cultural significance, such as guinea pigs, *Cavia porcellus,* were also occasionally buried rather than disposed of in midden refuse but these have not yet been found.

Though not always possible, these samples come from the early Ceramic age deposits on each island. The migration of people, originating from northern South America, progressed up the island chain reaching the Bahamas late in the prehistory of the Caribbean. The dates, associated with the contexts with which the faunal samples belong, reflect this progress up the island chain, with the Bahaman sites the most recent (Table 1).

One of the most important methods in zooarchaeological research is recovery of animal remains with fine gauge sieves (3 and 1.5 mm) (Payne 1972). Though this is by no means a new method, it has only recently been used in the West Indies. Faunal samples recovered with fine gauge screen give us a new improved view of animal catches in the West Indies. Based on old samples, recovered with large gauge sieves or simply gathered, one would conclude that sea turtles were the primary resource used in the Caribbean. However, with the new recovery methods it is now clear that prehistoric catches included diverse species and the majority were small individuals. The width of vertebral centra of fishes correlates well with the size of the fish in life and can be used as a gauge of the sizes of exploited animals. Most of the measurements of vertebral centra from West Indian samples range from 2 to 6 mm. These come from fishes estimated to weigh between 60 and 569 gms (Wing and Brown 1979). Only samples recovered with a fine gauge sieving strategy that would recover this important component of Caribbean faunas are included.

Identification and quantification.—Identifications are always made by direct comparison of each specimen with modern reference specimens in the collections of the Florida Museum of Natural History. The anatomical position of each fragment is determined first and then each fragment is identified to the lowest possible taxon. Identifications to the level of genus and family are used for this analysis to allow greatest possible comparability among samples. In general preservation is good as these remains are in calcareous deposits that provide alkaline conditions favorable for bone preservation. Therefore, identification of even the smallest and most delicate bones is usually possible.

We use minimum numbers of individuals (MNI) to quantify the animals represented in the samples. This measure is a count of the greatest number of identical elements for each taxon. The size of skeletal elements is taken into account in these calculations. For example, one taxon represented by five right dentaries and two left dentaries would represent at least five individuals (MNI) but, if one of the left dentaries is far larger than any of those on the right, the MNI estimate could be increased from five to six. As Grayson (1984) has correctly pointed out, adding the MNI from successive levels can bias the results by counting one carcass, spread though two levels, twice. This is less likely when the fauna is composed of small individuals. Nevertheless, our calculations of MNI are based on the individual animals from an occupation zone, a discrete feature, or widely separated levels.

We use MNI for this analysis for one important reason. These faunal assemblages are composed of species with different numbers of skeletal elements and if we used the basic method of quantification, a count of identified specimens (NISP), we would bias the results in favor of those species with the largest number of skeletal elements. For example, most fish skulls have approximately ten times the number of elements found in a mammal or bird skull and some animals have unique, abundant, and easily identifiable skeletal elements, such as the spines on the spiny box fish or the dermal bones of an armadillo. These differences bias the results of quantification based on NISP. Samples, composed of species from all vertebrate classes with different numbers of identifiable skeletal elements, need to be quantified in some way that reduces these innate biases. Calculation of minimum numbers of individuals is the best method we know at this time.

Sample size.—Sample size is always a critical issue because samples must be large enough to reflect accurately the nature of the population sampled (Table 2). However, it is not always possible to dictate the sizes of archaeological samples. We include only those that have over 125 MNI and then test the sample sizes to insure that the diversity measures we use in the analysis do not correlate with sample size. The methods we use to test for adequate sample size are the random sampling method and sample size rarefaction.

We use the random sampling method described by Kintigh (1989) and McCartney and Glass (1990) to test whether our samples are random collections from a population. We simulate random samples from the summed generic abundance for all sites together and count the number of genera "collected" for hypothetical sample sizes from 0–3,000. The distribution of these hypothetical samples shows a classic rarefaction curve where accumulation of new genera progresses at an increasingly slow rate with increased sample size. When the data from each site are plotted against this curve, we find that the sites from the two large islands, Hispaniola and Puerto Rico, and the site on the island closest to the mainland, Grenada, fall within the distribution while the cluster of sites from smaller islands falls significantly below the line (Fig. 2). This indicates that sites on large islands and the island close to the mainland are representative of the overall population in terms of sample size and generic richness, but the sites on smaller islands fall well below the expected richness even in the case of the large sample size for the site on Antigua. Species richness in the samples from the two smallest islands, Saba and Samana Cay, fall farthest below the line. This also indicates that island size effect on generic richness is large. Because of this island size effect on expected richness, it is also necessary to view sample size for each island separately.

We employ the method of sample size rarefaction to compare the adequacy of each of the samples (Sanders 1968; Hurlbert 1971; Krebs 1989). This procedure provides an estimate of the number of species that would be expected in a sample of a given size based on the relative abundance of species in the whole sample. We use this technique to produce rarefaction curves for each sample and then scale these curves to 1 for sample size on the x axis and for generic richness on the y

TABLE 2.—Islands, their land area (km^2), number of vertebrate genera identified, minimum numbers of individuals (MNI), diversity (H'), and log of the genera. The number of genera for each site or component of a site are listed after the total number of genera for the island.

Island	Area[1]	Number of Genera	MNI	H'	Log of Genera
Bahamas					
1. Samana Cay	39	23: 17 (SM-2), 12 (SM-7)	227	0.79	1.36
2. Crooked Is.	238	20: 11 (CK-8), 20 (CK-14)	196	1.02	1.30
Turks and Caicos					
3. Middle Caicos	190	36: 32 (MC-6), 19 (MC-12)	264	1.12	1.56
Greater Antilles					
4. Hispaniola	76193	48: 34 (fea. 4), 36 (fea. 25)	199	1.42	1.68
5. Puerto Rico	8865	45: 43 (S38W18), 22 (fea. 104)	153	1.43	1.65
Virgin Islands					
6. St. John	49	38: 34 (TB), 24 (KB)	249	1.28	1.58
7. St. Thomas	70	33	202	1.22	1.52
Lesser Antilles					
8. St. Martin	88	21	147	0.97	1.32
9. Saba	13	29: 23 (KR), 26 (SB)	196	1.27	1.46
10. Nevis	130	32: 30 (GE-5), 20 (GE-1)	234	1.22	1.51
11. Antigua	280	36	869	1.15	1.56
12. Barbados	431	27	179	1.18	1.43
13. Grenada	344	31	132	1.33	1.49

[1] Woods 1990

axis. The curves are then plotted for comparison (Fig. 3). The sample from Antigua, number 12, is the largest with 823 MNI and therefore shows a greater degree of saturation than the curves of the other samples, which are similar to one another.

The other critical issue about sample size, in addition to being an adequate representation of the animals that were central to the protein portion of the prehistoric diet, is whether they correlate with the measures used in this analysis, generic richness, diversity, and equitability. To test for correlation we use a Spearman's rank correlation of sample size (total MNI and marine component subsample) with generic richness and diversity. None of these correlations are significant, showing that total sample size is not linked to richness or diversity, nor are the marine subsamples linked to the marine component richness or diversity or the terrestrial subsample linked to terrestrial diversity (Table 3). However, terrestrial generic richness is correlated with terrestrial MNI, indicating that there may be a reduction in the power of our regression analysis for this group. As a conservative measure, we evaluate terrestrial subsamples in a descriptive sense only and focus on the relative importance of terrestrial fauna within the whole. These

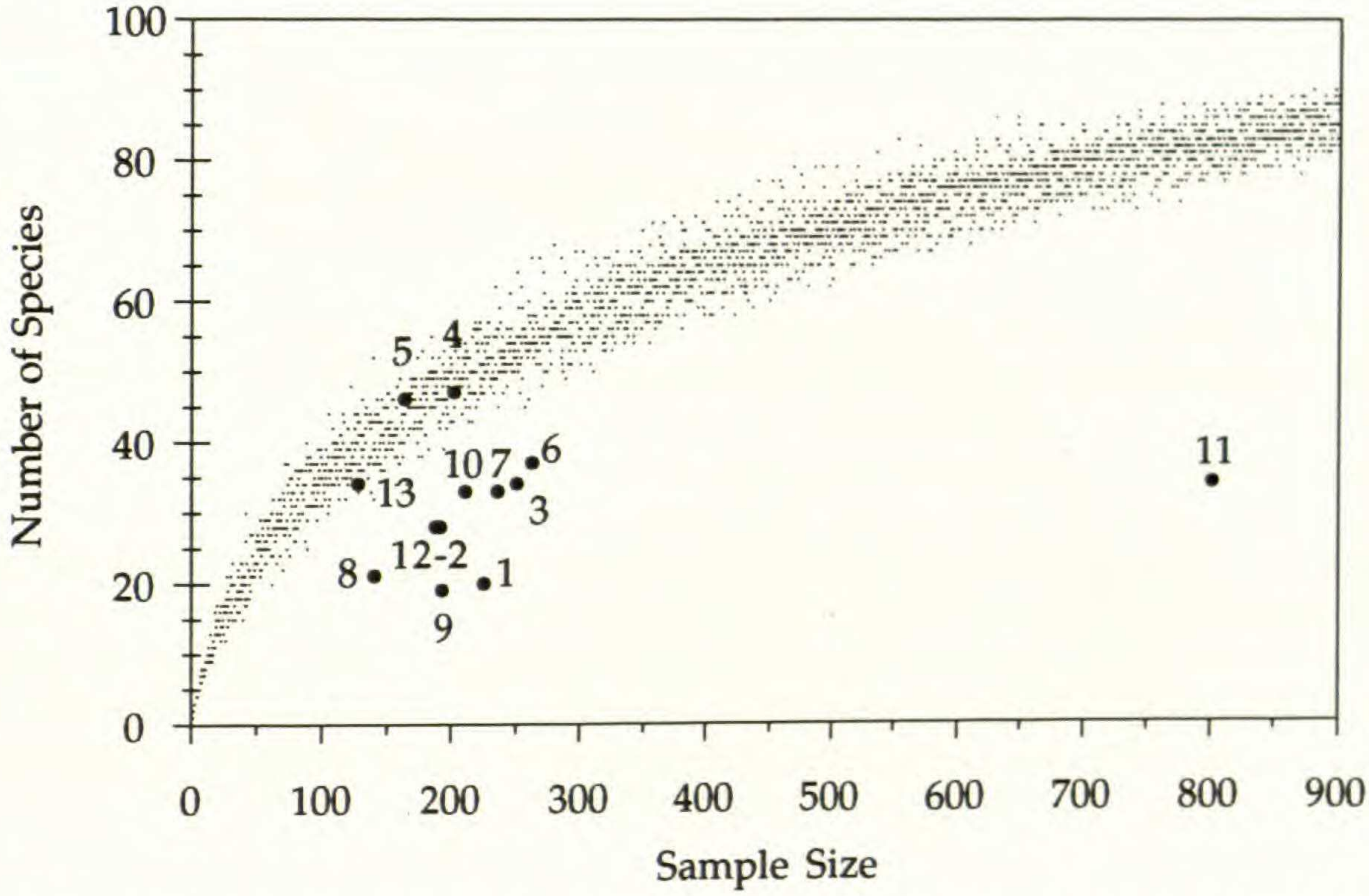


FIG. 2.—Simulated random samples from the summed generic abundance for all sites together, and a count of the number of genera "collected" for hypothetical sample sizes from 0 to 3000. Each point represents a hypothetical sample.

tests indicate that the sizes of the total samples we use adequately represent the animals that were central to the vertebrate animal protein portion of the diet of settlers on each island. Undoubtedly, other rare species were occasionally used and some of these may have had great cultural significance, but as subsistence is based upon the staples these samples fit our analysis requirements.

Diversity and equitability.—Ecologists frequently use measures developed from information theory (Shannon and Weaver 1949; Margalef 1958) to describe the diversity of biological systems (Peet 1974; Cowell 1978; Magurren 1988; Krebs 1989). These measures combine data on numbers of categories (taxa) and abundance within each category to describe the heterogeneity of a system. Diversity by this definition reflects the amount of uncertainty of predicting the identity of an individual picked at random from the community, i.e., the heterogeneity of the sample. For our analysis we use a common measure of heterogeneity, the Shannon-Weaver function (Shannon and Weaver 1949):

$$H' = \sum_{i=1}^{S} p_i \log_{10} (p_i)$$

where;

H' = information content of the sample
S = number of taxonomic categories
p_i = proportion of the total sample composed of individuals in the ith taxon

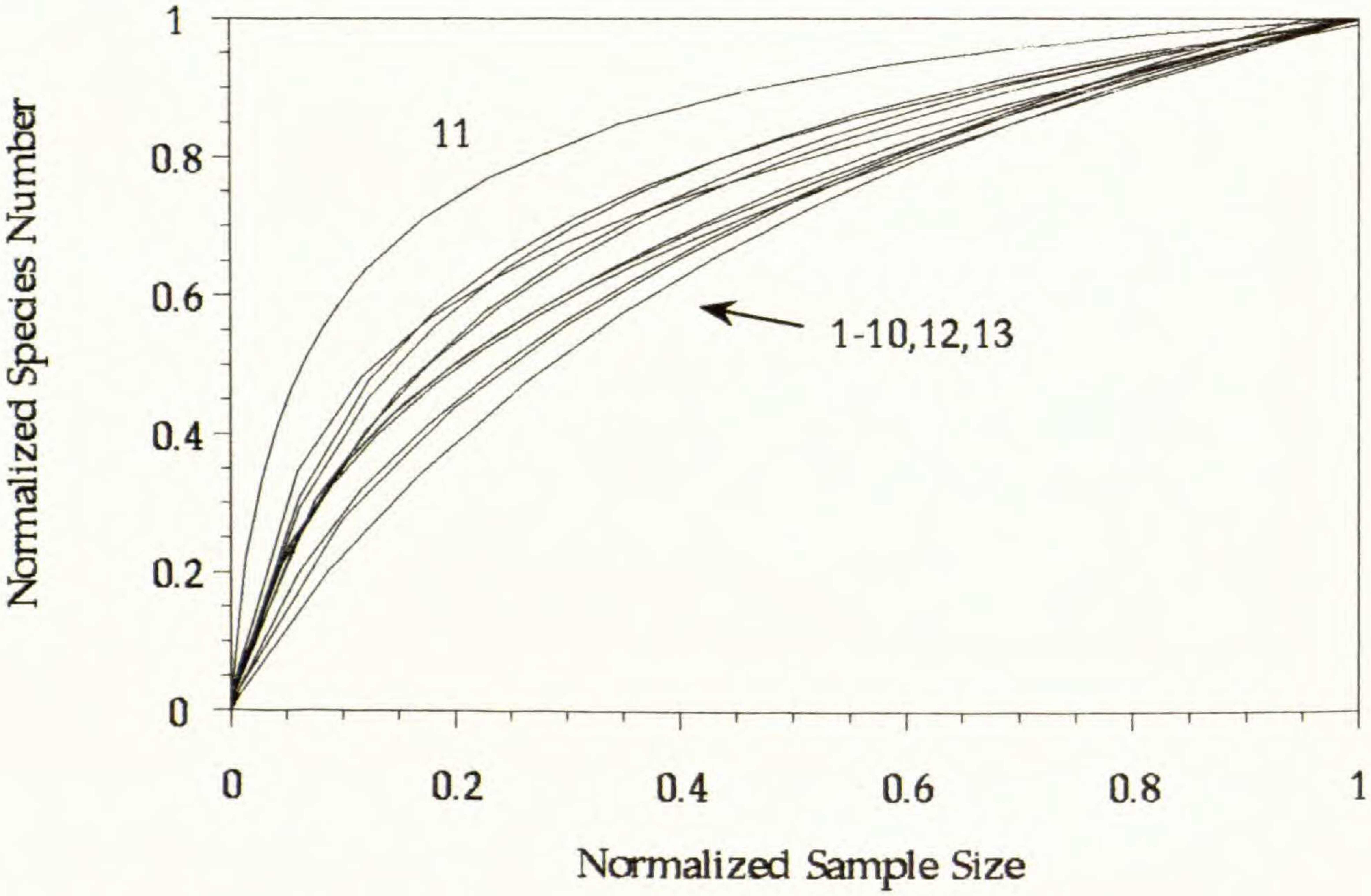


FIG. 3.—Normalized rarefaction curves for each site.

TABLE 3.—The statistical significance of the Spearman's rank correlation of whole sample size and subsample size with generic richness and diversity.

Comparisons		Probability	Significance
MNI	for the total sample vs.:		
	total generic richness	p = .1885	NS
	total diversity	p = .7747	NS
	marine generic richness	p = .3800	NS
	marine diversity	p = .5745	NS
	terrestrial generic richness	p = .3559	NS
	terrestrial diversity	p = .8902	NS
MNI	for the marine component vs.:		
	marine generic richness	p = .2418	NS
	marine diversity	p = .2882	NS
MNI	for terrestrial component vs.:		
	terrestrial generic richness	p = .0256	****
	terrestrial diversity	p = .5908	NS

With this measure of diversity, samples with an even distribution of abundance between taxa have higher diversity than samples with the same number of taxa but with disproportionately high abundance of a few taxa. Alternatively, diversity will reflect the number of taxonomic categories in all samples with equal distributions of abundance. More taxonomic categories lead to greater diversity values when samples show the same degree of equitability in abundance.

Measures of heterogeneity combine two independent concepts, species richness (the number of species) and equitability (the degree to which species are equally abundant). Examination of equitability independent of richness is also of interest. Equitability may be calculated by scaling the heterogeneity measure to its theoretical maximum (Hurlbert 1971; Peet 1974). The theoretical maximum for H' occurs at LogS, so equitability is measured by V'=H'/LogS (Hurlbert 1971). Values close to one suggest even use of resources, while lower values suggest a greater degree of specialization in the use of resources. Low values may occur because of low available diversity of food resources or because of specialized use of a few taxa among a highly diverse sample of food resources.

Similarity indices.—Similarity measures describe the overlap in the use of resources, in other words, the similarity between the faunal assemblages of two sites. We use the simplified Morisita-Horn index (MH) to compute the similarity of the faunal samples from different islands (Horn 1966). The index is a function of the overlap in taxonomic categories and abundance within each category. It is computed as follows for site a and b:

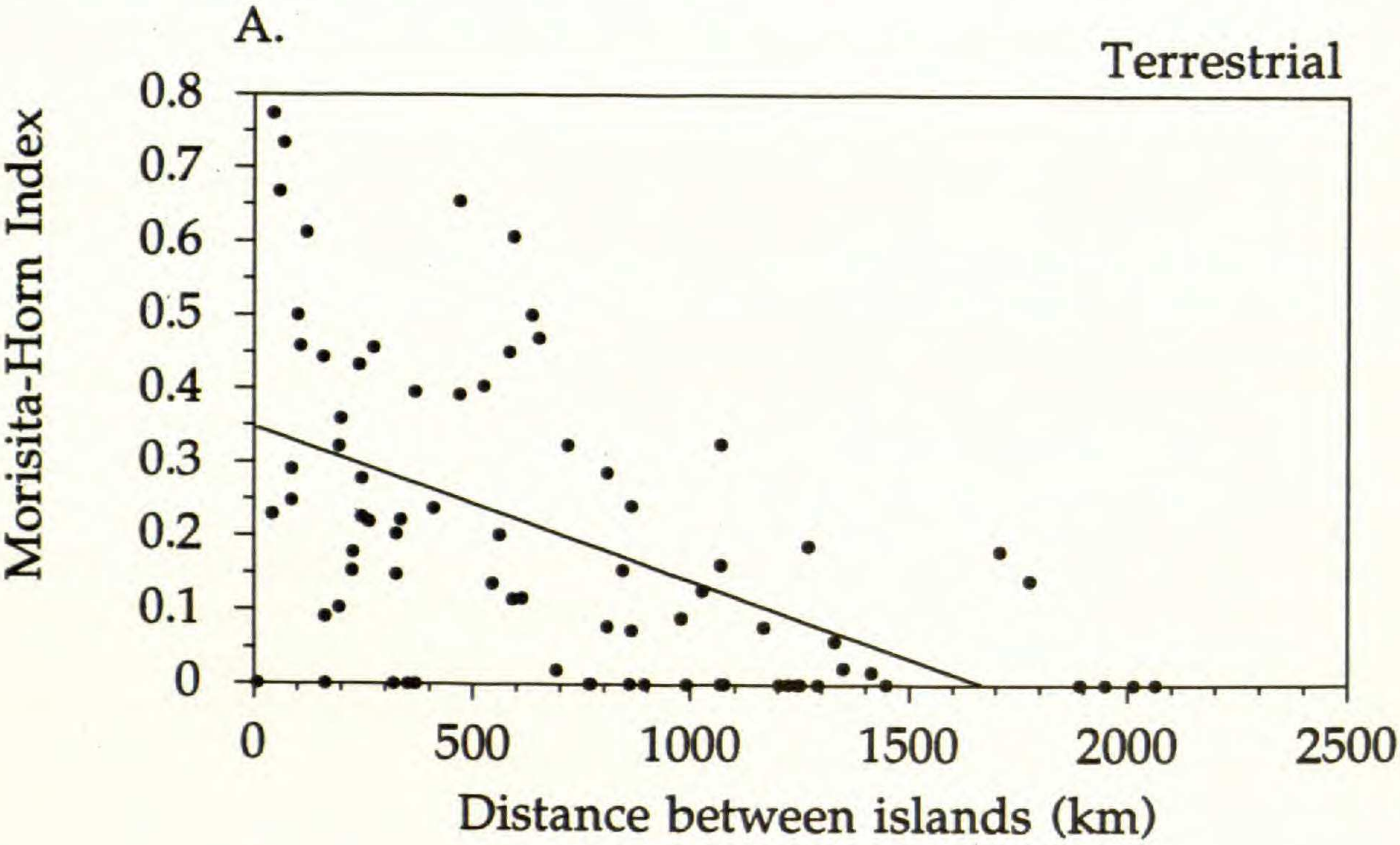
$$MH = 2 \left[\frac{aN_i bN_i}{(da+db)N_a N_b} \right]$$

where;

N_a = total number of individuals in site a
aN_i = number if individuals in the i^{th} species of site a
d_a = sum of aN_i^2 divided by N_a^2

This index is generally insensitive to differences in the richness of taxonomic categories and sample size but sensitive to the abundance of the most numerous taxonomic category (Wolda 1981). Independent studies by Smith (1986) and Wolda (1981) found that the Morisita-Horn index is among the most sensitive and robust of measures available. The insensitivity of the index to differences in sample size makes it particularly appropriate for this analysis.

We use this similarity index to compute the scale of taxonomic overlap for the marine and terrestrial subsamples separately. This is done by plotting all pairwise comparisons between marine and terrestrial subsamples and the distance between each pair of islands from which the subsamples are derived (Fig. 4a and 4b). We expect that the typically large scale of dispersal of organisms in the sea will result in a relatively high degree of overlap in the taxonomic categories within the marine subsamples association between similarity and distance between islands. In contrast, the restricted dispersal of terrestrial organisms within typical island archipelagos will reflect generally low values for similarity and decreasing similarity with increased distance between islands. This pattern



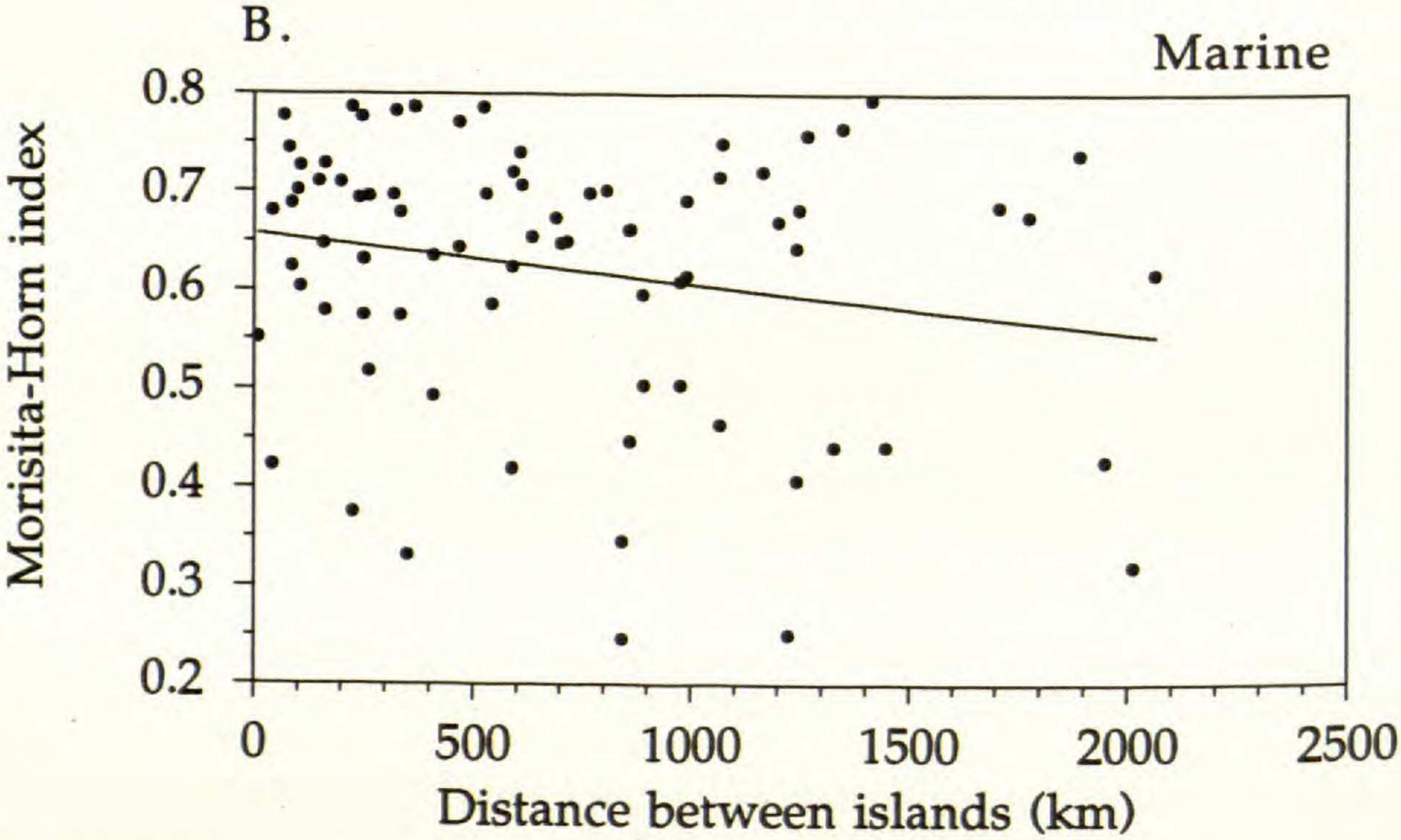


FIG. 4a.—Morisita-Horn index of the similarity between terrestrial components of each site measured against the distance between islands (km). ($y = 0.6572 + -0.00020823x$; $r = 0.53$; $p < .05$). FIG. 4b.—Morisita-Horn index of the similarity between marine components of each site measured against the distance between islands (km). ($y = 0.6572 + -0.0000503x$; $r = 0.19$; $p > .05$ NS).

reflects the fundamental difference between open marine systems (in the sense of Roughgarden et al. 1985) and the subdivided terrestrial systems, islands.

Log species/log area curves.—The animals used by people do not reflect the total island fauna or the relative abundance in which they occurred. Rather, human exploitation may be viewed as a filter retaining the remains of those species that were selected for food and could be caught with the available technology. Though faunal assemblages represented by remains may be modified by a number of other filters, such as the depositional history, preservation, and identifiability of the remains, we do not expect these filters to be sensitive to differences in island size or distance from the mainland between sites. However the first filter, the effect of species diversity and abundance on human foraging patterns, may retain properties consistent with the available resources on each island. That is, we expect the slope of log species/log area curve for the sites to be positive, reflecting the slope of log species/log area curves for most distributions of organisms that fall within relatively narrow limits, a range between 0.2 and 0.4 (Connor and McCoy 1979). However, if there was some differential selectivity or enhancement of resources on small islands, this slope would be reduced.

In the migration into ever more distant and isolated islands, several adjustments may have been made to allow sustainable harvests of animal resources. One modification is to emphasize use of more reliable resources, such as reef fishes. Another made by people who colonized most islands is to enhance the number of terrestrial species through the introduction of domestic and captive animals brought from the mainland or from nearby islands. Such additions to the exploited faunas of small islands would reduce the slope of the total log species/log area curve.

Analysis.—Our strategy is to analyze the total faunal samples for patterns of diversity, equitability, similarity, and the slopes of the log species/log area curves, and then to divide the samples into habitat specific subsamples to determine the pattern of distribution of each subsample in a descriptive sense. We test for trends associated with distance from the mainland and island area with least square linear regression analysis. In the case of diversity and equitability measures, which are not necessarily normally distributed, we use the more conservative approach of rank transforming the index and running a regression on the ranked estimates (Conover 1980).

Subsamples.—For analysis of trends within the fauna, we divide the samples into four habitat specific subsamples, which are composed of endemic and introduced terrestrial species, estuarine, and reef organisms. We investigate trends in generic richness and relative size (MNI) between the subsamples associated with distance along the island chain and island area. Unfortunately, by dividing the total samples into these groups the sample sizes of terrestrial and introduced animals are compromised for regression analysis. We therefore rely on a more descriptive analysis of distribution of these two groups. The endemic terrestrial faunas of the islands were enriched by the animals introduced by Amerindians from both the mainland of South America and the Greater Antilles (Table 4). Though we examine the importance of introduced animals to subsistence, they probably had significance beyond subsistence (Wing 1993a). The estuarine subsample includes; manatee (*Trichechus manatus* Linnaeus), West Indian monk seal [*Monachus tropicalus* (Gray)], crocodile (*Crocodylus* sp.), sea turtle (Cheloniidae), sting ray (*Dasyatis* sp.), ladyfish (*Elops saurus* Linnaeus), tarpon (*Megalops atlanticus* Valenciennes), bonefish [*Albula vulpes* (Linnaeus)], herrings (Clupeidae), needlefishes

TABLE 4.—Introduced animals in the Caribbean during prehistoric times (Olson 1978; Morgan and Woods 1986; Wing 1989).

Source	Destination	Species
Within Island Chain Introductions		
Hispaniola	Puerto Rico, Virgin Islands	extinct insectivore *Nesophontes edithae* Anthony hutia *Isolobodon portoricensis* Allen flightless rail *Nesotrochis debooyi* Wetmore
Greater Antilles	Bahamas, San Salvador Lesser Antilles, Saba	pond turtle *Trachemys* sp.
Large Bahama Is.	remote Bahamas, Samana Cay	? cony *Geocapromys* sp.
Introductions From Mainland		
South America	probably entire Caribbean	domestic dog *Canis familiaris* Linnaeus
South America	Lesser Antilles	opossum *Didelphis marsupialis* Linnaeus armadillo *Dasypus novemcinctus* Linnaeus agouti *Dasyprocta leporina* (Linnaeus) tortoise *Geochelone carbonaria* Spix[1]
South America	Antigua, Puerto Rico Hispaniola	guinea pig *Cavia porcellus* (Linnaeus)

[1] probably an historic period introduction.

(Belonidae), silversides (Atherinidae), snook (*Centropomus* spp.), bigeye scad [*Selar crumenophthalmus* (Bloch)], amberjack (*Seriola* sp.), mojarra (Gerreidae), barred grunt [*Conodon nobilis* (Linnaeus)], pigfish [*Orthopristis chrysoptera* (Linnaeus)] porgies (Sparidae), croacker (Sciaenidae), mullet (Mugilidae), clinids (Clinidae), sleeper (Eleotridae), cutlassfish (*Trichiurus lepturus* Linnaeus), and boxfish (*Lactophrys* spp.) (Randall 1968). Pelagic fishes are a rare component of these faunal assemblages, never constituting more than 7.5% of the fauna. Thus we do not analyze this component separately. The group of fishes inhabiting reefs and the surrounding pelagic waters includes all other marine genera (Randall 1968). The taxa represented in all of the samples are listed in Appendix 1.

RESULTS

Whole Samples.—We apply three methods of analysis to the whole samples representative of each island. These are correlations between diversity indices and generic richness with island area and the measure of equitability with distance

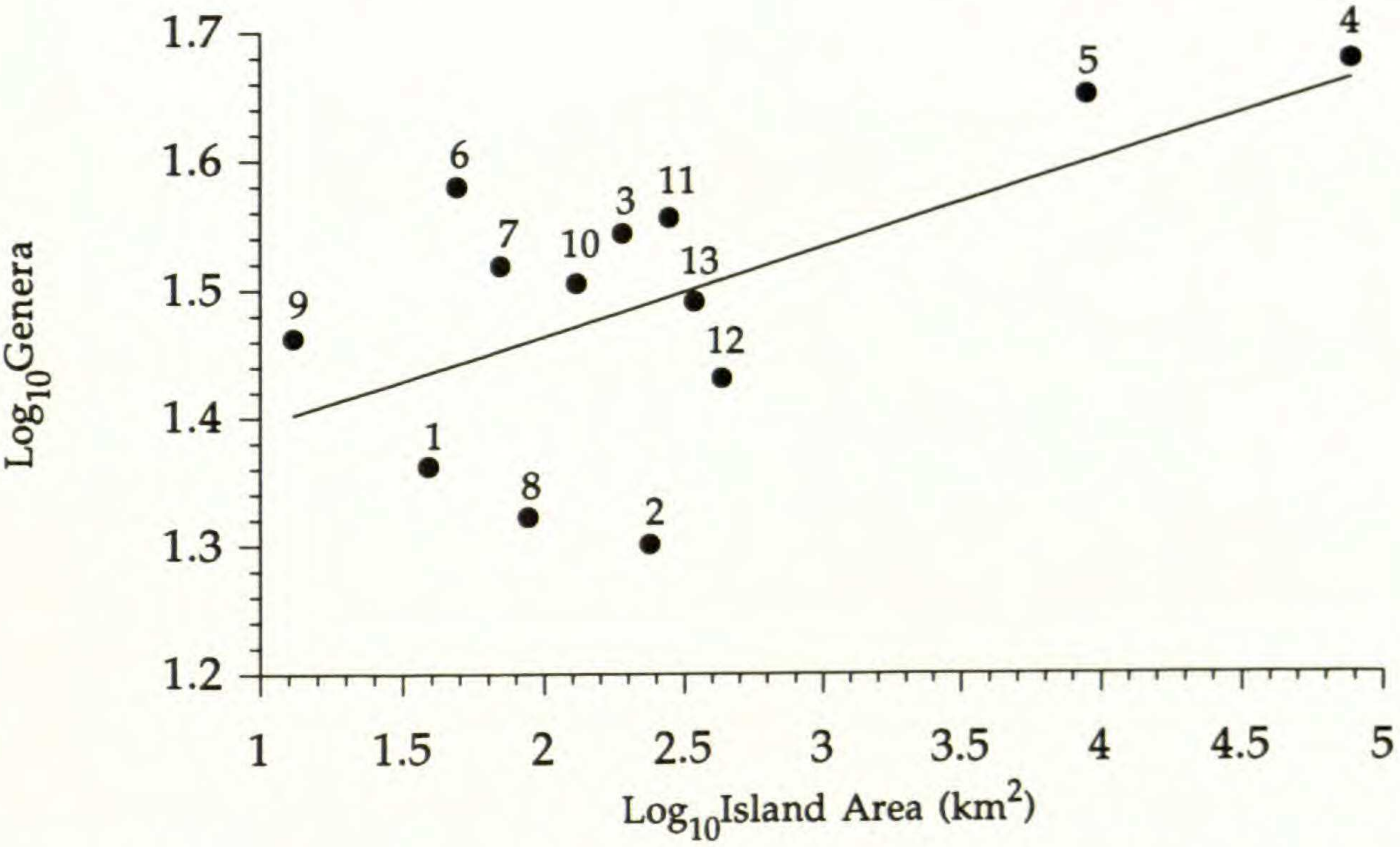


FIG. 5.—Log_{10} of the genera of the whole sample plotted against the Log_{10} of the area of the island. ($y = 1.3234 + 0.07018x$; $r = 0.601$; $r^2 = 0.362$; $p = .0296$).

from the mainland. No significant correlation exists between the total sample size and each of these tests as measured by the Spearman's rank correlation.

We find that the log species/log area curve (Fig. 5) increases with island area. The slope of the curve is 0.07, lower than predicted by data from the underlying distribution of fauna on islands, which ranges between 0.2 and 0.4 (Connor and McCoy 1979). This illustrates the effect of human selection from the underlying distribution of animals on islands of different sizes. The logs of the numbers of taxa fall into groups according to the location of the island rather than strictly by island size (Table 2). The samples from the Bahamas and those from the Lesser Antilles are broadly overlapping, 1.30 to 1.56. The values for the samples from the two Virgin Islands sites, 1.52 and 1.58, are at the upper end of the range, while those from the Greater Antillean sites are well above that range, 1.65 and 1.68.

A similar pattern of increase with island area results from diversity, as measured by the Shannon-Weaver index (Table 2, Fig. 6). Regression analysis of these data produces a line with a positive slope, 0.0809, that is statistically different from zero. The ranked diversity measures and regression produce the same pattern. As with the log species/log area curve, the samples from the Greater Antillean sites (Hispaniola and Puerto Rico) have distinctly more diverse faunas, with diversity values of 1.42 and 1.43, than the cluster of samples from the Lesser Antilles and the Virgin Islands, with values from 0.97 to 1.33. Samples from sites in the Bahamas fall below the regression line, having the lowest diversities, with values from 0.79 to 1.12.

Analysis of the equitability of the whole faunal samples results in a significant pattern of decreased equitability with distance from the mainland (Fig. 7). The equitability indices are high, above 0.8 for the majority of the samples from

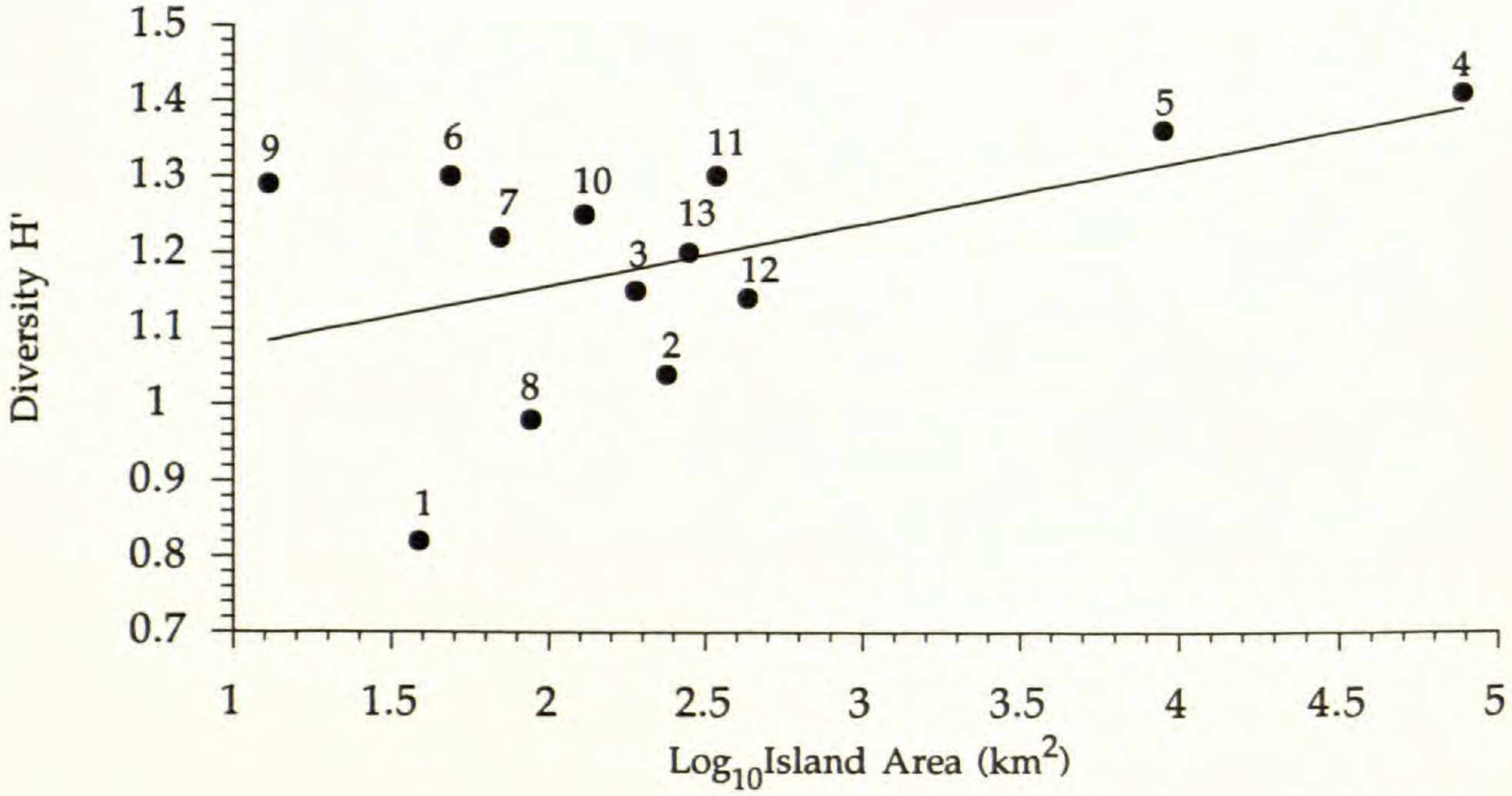


FIG. 6.—Diversity (H') of the total sample plotted against the Log_{10} of the area of the island. ($y = 0.9936 + 0.0809x$; $r = 0.49$; $r^2 = 0.244$; $p = .086$ NS).

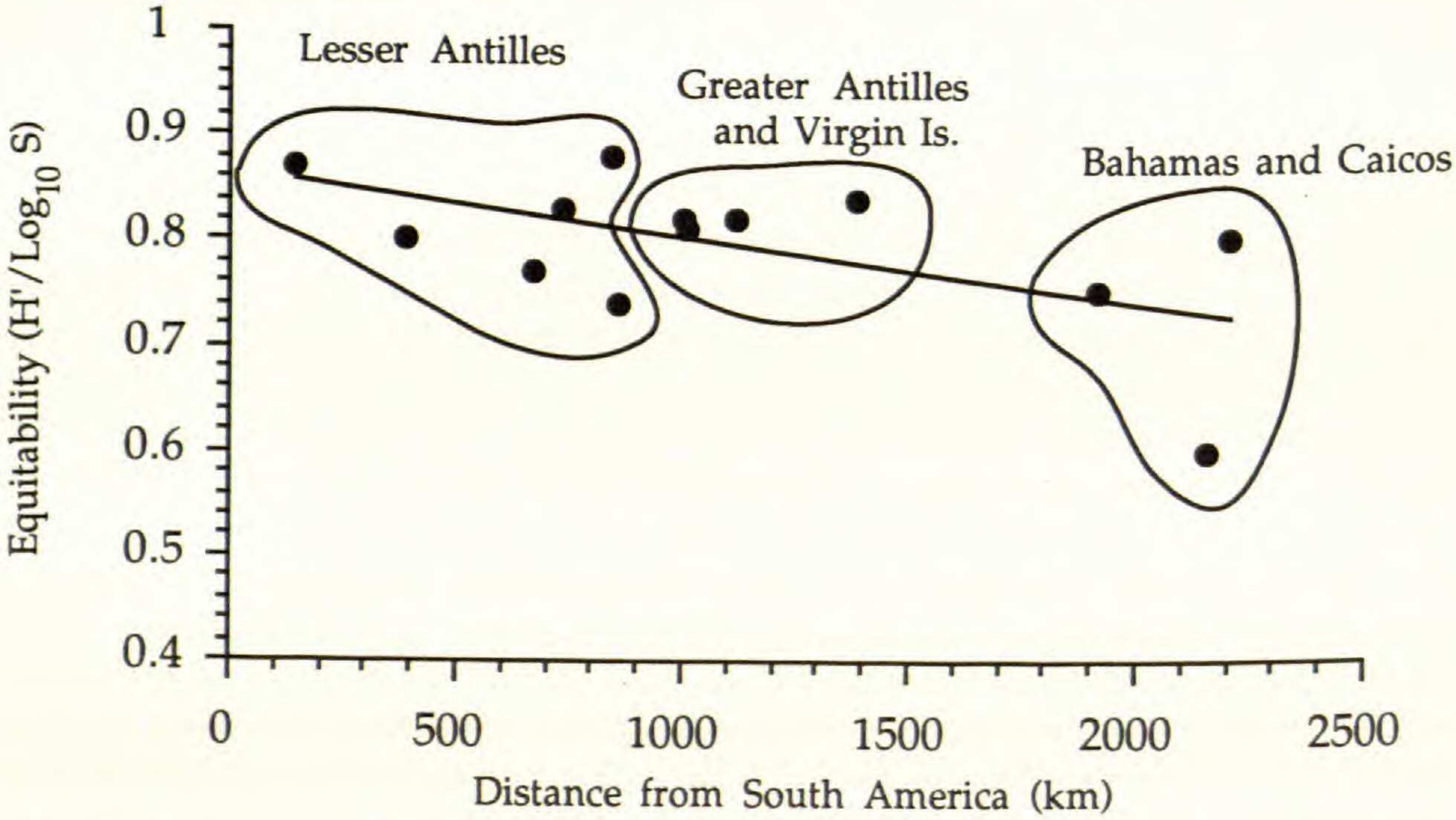


FIG. 7.—Equitability of each whole sample plotted against distance from the mainland of South America. ($y = 0.86 + -0.0000629x$; $r = 0.56$; $r^2 = 0.32$; p .0433).

the Lesser and Greater Antilles and the Virgin Islands, and at 0.8 or substantially below for the samples from the Bahamas and Middle Caicos.

Similarity between island faunas.—The Morisita-Horn similarity indices for the marine and terrestrial components of the samples provide evidence for the differences between these two components in terms of similarity across the island chain. This index of similarity reveals two trends that meet our expectations.

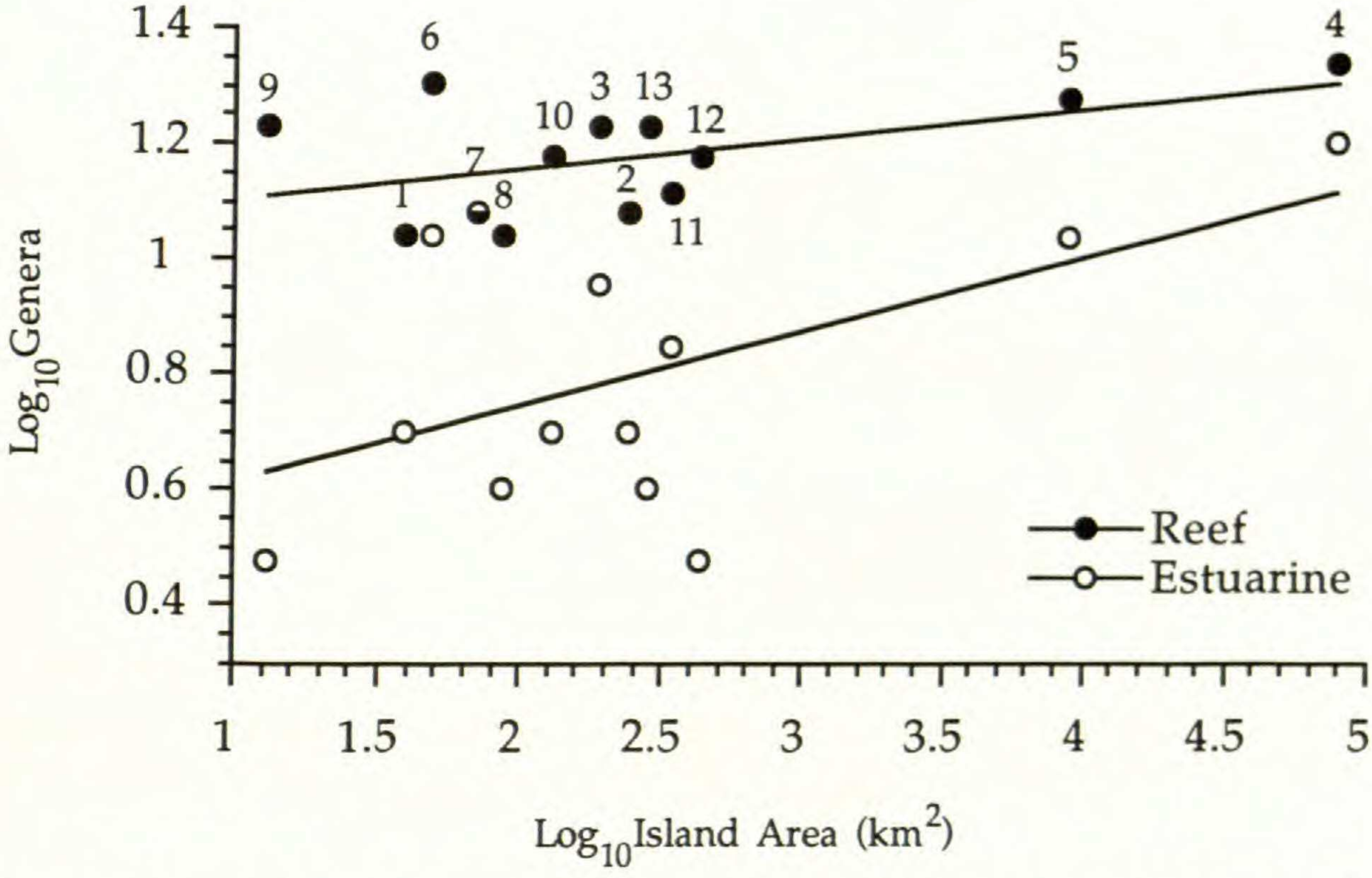


FIG. 8.—Log_{10} of reef genera (a) and estuarine genera (b) plotted against the Log_{10} of the area of the island. a: ($y = 1.053 + 0.0519x$; $r = 0.517$; $r^2 = 0.268$; $p = .069$ NS) b: ($y = 0.486 + 0.130x$; $r = 0.540$; $r^2 = 0.3$; $p = .05$).

Among the terrestrial subsamples, increased distance between islands from which the pairwise subsamples were taken is correlated with decrease in similarity. The resulting regression produces a statistically significant line of negative slope (Fig. 4a). However, among the aquatic subsamples, distance between islands is not correlated with similarity. The resulting regression produces a line with a slope not significantly different from zero (Fig. 4b). The pairwise overlap values are not strictly independent, so confidence limits established by regression must be interpreted cautiously. However, the trends show clearly that the marine component of the faunal samples is more similar across the island chain than the terrestrial component.

Habitat specific subsamples.—Further subdivisions of the faunal samples allow examination of those segments of the faunal assemblage most effected by island size and isolation. The marine component of these samples is subdivided into estuarine, reef, and pelagic animals and each is correlated with island area in a transect from the South American mainland to the Bahamas. Pelagic fish richness and abundance are low in all samples, but highest in the two most oceanic islands, Samana Cay and Barbados. Reef richness and abundance vary little throughout the island chain. The log species/log area curve for the reef fauna alone has a slope that is not significantly different from zero (Fig. 8). In contrast, estuarine generic richness is greatest in the larger islands of the Greater Antilles and their immediate neighbors, the Virgin Islands and Middle Caicos. The log species/log area curve for the estuarine fauna alone has a significant slope of 0.130. This difference in the slope is the direct effect of island size on the richness

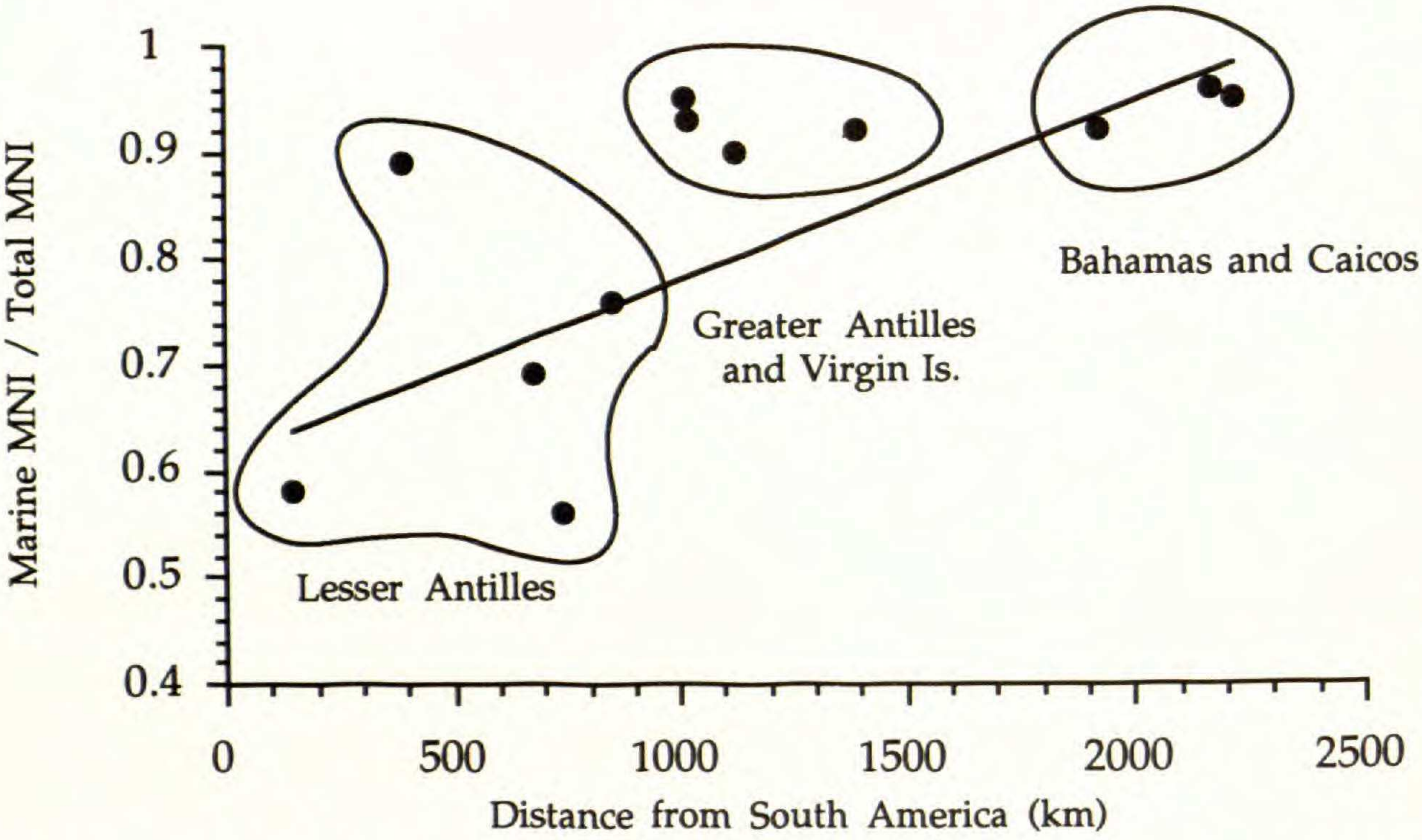


FIG. 9.—The MNI of marine genera divided by the total MNI plotted against the distance from the mainland of South America. ($y = 0.6117 + 0.0001\,68x$; $r = 0.57$; $r^2 = 0.057$; $p = .04$).

of estuarine fauna, which disproportionately enriches the marine subsample on large islands.

Another aspect of the marine component is the equitability of the marine fauna compared with distance from the South American mainland. Equitability of the marine fauna decreases with distance from the mainland. The regression of these equitability measures against distance from South America produces a statistically significant line with negative slope. This does not differ significantly from the equitability of the whole samples. Both patterns reflect a general trend towards specialization on marine resources, particularly in the distant Bahamian islands.

The ratio between marine MNI and total MNI provides evidence for the relative importance of the marine faunal component, and by extension the terrestrial component. The correlation of this ratio with distance from the South American mainland produces a statistically significant regression line with a positive slope of 0.0002 (Fig. 9). The samples from the Lesser Antilles form a group with relatively more terrestrial animals, and therefore a low ratio of marine to total individual animals (0.38 to 0.76, excluding Barbados). The outlier to this group (0.89) is the site on Barbados, which is the most oceanic island in the Antilles. The Greater Antilles have intermediate ratios of marine to terrestrial MNI (0.90 to 0.92). The Virgin Islands and the Bahamas have the highest ratios (0.92 to 0.96) and the ratio for the sample from Middle Caisos (0.92) is within this range. These trends suggest an increase in dependance on marine animals with distance from the mainland, with island size and isolation also playing a part.

The terrestrial faunal component is smaller than the marine component and is composed of endemic species and introduced animals. The results of a log species/log area regression fails to reveal a significant relationship. However, several patterns exist in the richness and abundance of the terrestrial faunal component. The source of introduced animals is from the mainland of South America and from the Greater Antilles (Table 4). Consequently, introductions of the most genera are to Grenada, closest to the mainland, and St. Thomas, closest to the Greater Antillean source. The two smallest islands, Saba and Samana Cay, have more introduced genera than the islands adjacent to them (Fig. 10a). This pattern is also evident from the relative MNI of introduced and endemic animals along the island chain, which shows relatively high numbers of introduced animals near the mainland (Grenada and Barbados) and near the Greater Antilles (St. Thomas and St. John) (Fig. 11).

DISCUSSION

These results indicate that human exploitation of animal resources was not free from the constraints described by island biogeographic models. By every measure the trends are for greatest diversity on larger islands, the Greater Antilles, and the island closest to the mainland, Grenada, with lowest diversity on the smaller and most isolated islands of the Bahamas, Turks and Caicos. As a part of these trends, the relative importance of terrestrial resources diminishes with distance from the mainland, and the numbers of estuarine species increase with the island size. The slope (0.07) of the species/area curve by comparison with the range of slopes (0.2 to 0.4) for the underlying distribution of fauna on islands is below what would be anticipated if nothing were lost from the archaeological record and no human selection of resources took place (Connor and McCoy 1979). However, selection of resources and the fundamental choice of site location have an effect on how well the samples conform to the biogeographic principles.

A general observation is that island groups share characteristics and cluster in these analyses, and these relationships are statistically significant. The clusters we recognize are samples from the Lesser Antilles, the Greater Antilles, and the Bahamas; those from the Virgin Islands and Caicos appear to cluster more closely with the Greater Antilles in some analyses and with the Lesser Antilles and Bahamas in others. Thus, we do not see a trend of decreased diversity between the samples from Grenada and Barbados, close to the mainland, and Saba and St. Martin, farthest from the mainland within the Lesser Antilles. But as a group the samples from the Lesser Antilles are less diverse than those from the Greater Antilles. Least diverse of all are the group of samples from the Bahamas, Turks and Caicos. It is, therefore, more accurate to speak of clusters composed of variable samples, which as clusters conform to biogeographic expectations.

The variation within a cluster seems to relate to the particular choices made in selection of the home site and the complex of resources closest to the site. Choice of the location of the home site was not an arbitrary decision, and the majority of sites in the Caribbean and in our samples are located directly on the coast. Only two of the 18 sites are located inland. The Hope Estate site on St. Martin and the Tutu site on St. Thomas are both located 2 km inland. The Hope Estate sample deviates most from the other Lesser Antillean samples. Probably as a consequence of the inland location, the people at Hope Estate relied more on terrestrial

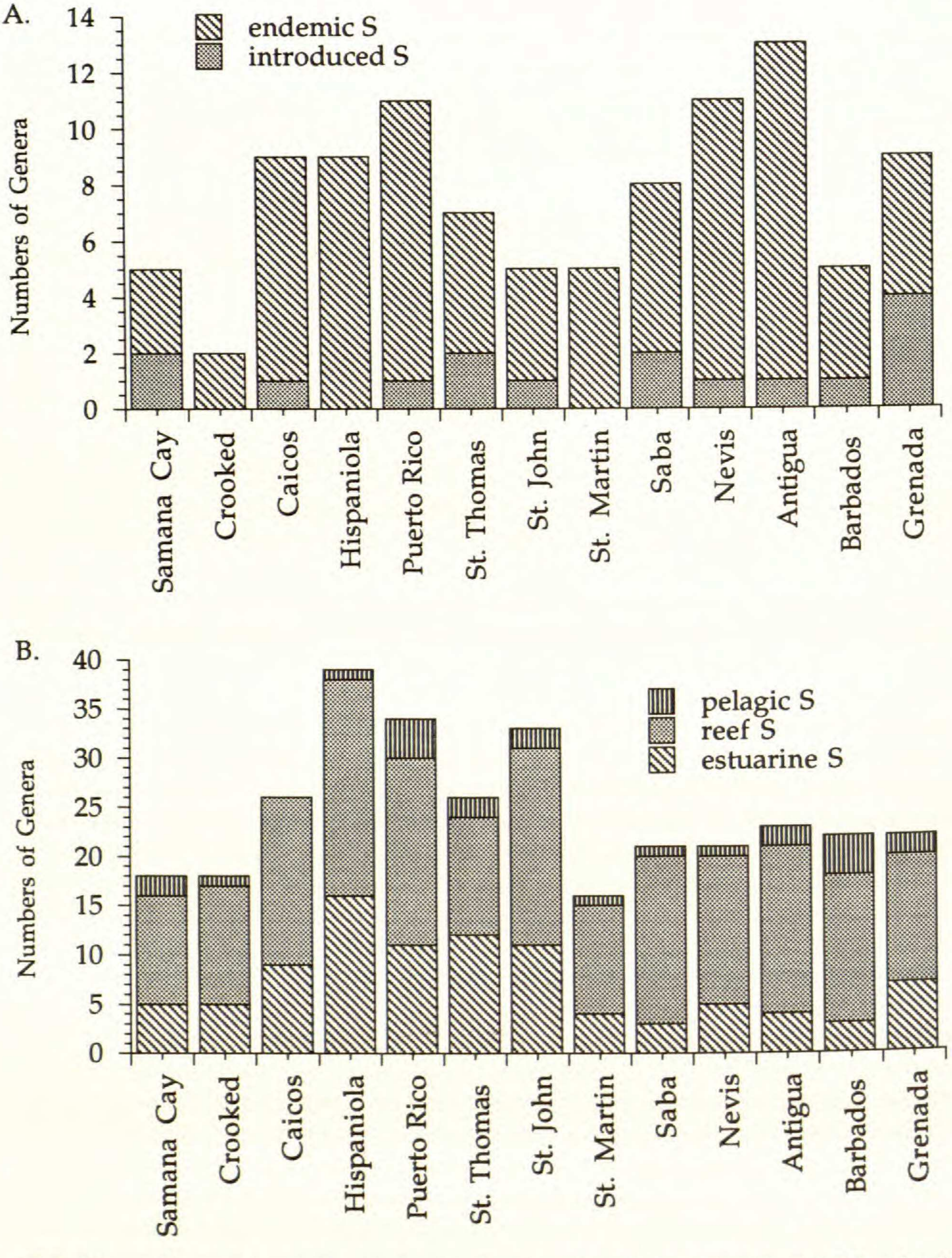


FIG. 10a.—The numbers of genera of introduced and endemic terrestrial animals presented on a gradient from Samana Cay to Grenada. FIG. 10b.—The numbers of genera of pelagic, estuarine, and reef animals presented on a gradient from Samana Cay to Grenada.

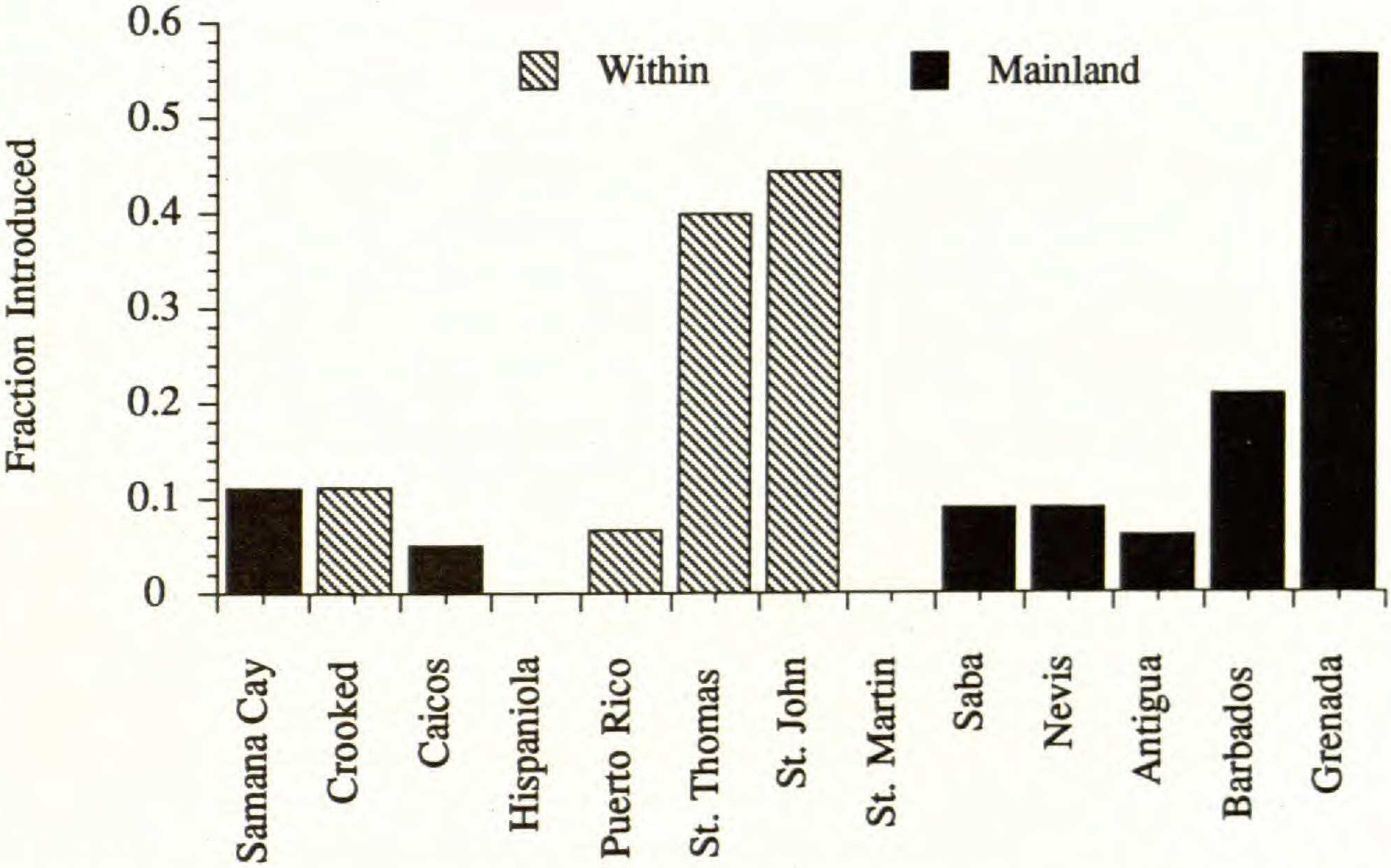


FIG. 11.—The fraction of introduced animals that were introduced from within the West Indian islands and from the South American mainland presented on a gradient from Samana Cay to Grenada.

vertebrates, rice rats, pigeons, and thrashers rather than a whole diverse array of reef fishes. Because of the reliance upon these three terrestrial species, the diversity of this sample is correspondingly low (0.97). The inland sample from St. Thomas does not exhibit the same degree of exploitation of terrestrial animals. Two of the terrestrial species, the insectivore *Nesophontes* and the hutia *Isolobodon*, are introduced species from the Greater Antilles, but neither were used intensively (Wing et al. 1993). The hutia increases in importance in subsequent occupations at Tutu and is more abundant in the later ceramic period site of Calabash Boom on the neighboring island of St. John.

Another example of the impact of site location on animal exploitation is in the difference between the two samples from Middle Caicos, one (MC-6) on the south side of the island facing the large lagoon known as Caicos Bank, formed by the arc of the Caicos islands, and the other (MC-12) on the north side of Middle Caicos facing an island shelf with extensive coral reefs. The faunal composition of these two sites reflects the resources of these locations, one with more estuarine species augmented by shore birds, and the other with more resources from the reefs. Differences such as these that relate to the location of sites undoubtedly account for the variability within the clusters of samples.

With this variation in mind, we can describe and compare the characteristics of the cluster of samples from Lesser Antilles, the Greater Antilles, and the Bahamas. The Lesser Antillean cluster has intermediate diversity, with Hope Estate having the lowest and the Pearls site on Grenada having the highest diversity within the cluster. Generic richness is also intermediate, with a mean number of

30 taxa and a range from 21 to 34. The ratio between marine and terrestrial MNI is low, reflecting the relatively greater dependence upon terrestrial animals. These terrestrial species, as at Hope Estate, are primarily rice rats, pigeons, thrashers, iguanas, and shore birds. This relatively greater reliance upon land animals at coastal sites may be an adherence to mainland traditions by the early colonists. Possibly through experience gained from migration further from the mainland, the shift to greater reliance upon marine resources could be made at least among coastal inhabitants.

Equitability of marine resources, excluding estuarine species, is high among both the Lesser and Greater Antillean samples. This shows a broad use of diverse reef fishes. This is what would be expected if either nets or traps were used. Traps are the more likely technique among reefs. Traps typically catch a variety of species, providing a wide choice to the fisherman. Both nets and traps can be constructed of fine gauge mesh making it possible to catch the small individuals represented in the samples.

The cluster of Greater Antillean samples differs in several respects from other clusters. These islands are large and exhibit the most faunal diversity. The samples from these large islands have intermediate equitability between the Lesser Antillean and Bahamian clusters. The characteristics that set them apart are the greater richness and abundance of the estuarine component of the faunas. The greater number of estuarine species is in large part responsible for the greater diversity in this cluster of samples. Large estuarine areas are associated with the river drainage from the large land masses, providing a greater extent of this habitat and, therefore, greater opportunity to exploit the resources living in estuarine habitats. The Greater Antilles, with their richer endemic fauna, was the source of several species that were kept in captivity and introduced to neighboring islands.

The Virgin Islands, between the Lesser and Greater Antilles, share many of the characteristics of the Greater Antillean cluster. The Virgin Islands, except for St. Croix, are on a shallow shelf that at lower sea level during the Pleistocene joined the land mass of Puerto Rico. Virgin Islands are small today and were the same size at the time they were occupied by the Amerindians. Their location, in shallow waters with more abundant estuarine fauna and close to the Greater Antilles, a source for animals that were introduced, are factors responsible for their high diversity. Most important among these introduced animals was the hutia, *Isolobodon portoricensis.* Despite access to terrestrial resources from the Greater Antilles, the Virgin Island samples have relatively more marine organisms, approaching the abundance of the marine samples from the Bahamas.

The marine component is the most important in the Bahamian, Turks and Caicos cluster. Terrestrial species are the least important, despite the presence of a large endemic rodent, *Geocapromys,* in the Bahamas. This rodent is present in the samples from each island but not abundant in any. Shallow lagoons with inshore estuarine species also occur in the Bahamas, as is evident in the sample from MC-6. Other than the intensive use of estuarine species at this site, the samples from the Bahamas form a cluster most different from that of the Greater Antilles. Both diversity and equitability are lowest in the Bahamian cluster. The equitability in the marine fauna is the lowest in this cluster, in other words fishing was the most specialized. The most abundant reef fish among these samples are the parrotfishes. If traps were used and caught the typical diversity of species, then some selection must have been practiced by the fishermen.

The most common endemic terrestrial species are on the small end of the size range of the majority of the fishes encountered in these West Indian sites. The smaller West Indian rice rats that lived in the northern Lesser Antilles weighed approximately 150 gm, which is larger than our North American species (Wing 1993b). The species that lived in the southern Antilles were still larger. The mourning doves average the same 150 gr, whereas the pigeons, members of the same family, are somewhat larger. Most of the fishes are estimated to range in size from 60 to 500 gm. Therefore, a predominance of land vertebrate, as is seen at Hope Estate, would have provided slightly less meat per animal than an economy based more intensively on marine vertebrates. Introduced animals such as agouti and hutia are all larger, weighing between 1 and 2 kg. Dogs were probably not eaten, but represent the largest land animal important to the Ceramic period culture.

How does this help us understand the problems that were faced by the early Ceramic age colonists of the West Indian archipelago? The variation within the recognized clusters reveals flexibility in the food quest within the constraints of the islands' resources. Mass capture fishing methods must have been used to obtain the array of species, and the consistent small size of the individuals in the catches suggest that fishing equipment was constructed of fine gauge mesh. Probably both traps and nets were important equipment and attained different degrees of importance depending on the extent of inshore estuarine waters and coral reefs adjacent to each island. The few large fishes in Caribbean samples were probably caught by other fishing methods. Thus, this flexibility suggests adaptable fishing strategies that took advantage of whatever resources were most readily available and reliable

The one means by which people augmented the resources of the land was through the introduction of animals. The source of these was from the mainland or from larger islands to smaller ones. Other than domestic dogs and guinea pigs, the introduced animals were captive, presumably tame, animals. These introductions are not numerically important in the samples included in this analysis, though hutia do predominate in at least some inland site in Puerto Rico and in a later ceramic period site in the Virgin Islands. Since domestic animals are not abundant in food refuse, perhaps they filled some other function. We know that guinea pigs have a long history of importance in the ritual and medicinal traditions in the Andes. Guinea pigs are also renowned for their high reproductive rates. Yet, when we find them in the Caribbean, their remains are present in widely separated islands but are rare where they are found. Their scarcity suggests that they were not important to the prehistoric diet, but they were probably used for other cultural purposes. The other introduced animals may also have played some role other than purely a subsistence item in Caribbean culture. Since many of these introduced animals were not domesticated, the maintenance of some of them in captivity may have been difficult, accounting for the small numbers of their remains in the refuse. However, two animals, the agouti and the hutia, were widely distributed by people, suggesting that their successful care and feeding was well understood.

What implications do these findings from the islands have for a better understanding of human use of mainland resources? Island biogeographic models were initially applied to actual islands, and then extended to studies of the faunas and floras of habitat islands. Habitat islands in this sense are habitats surrounded by a dramatically different environment, such as an old growth forest totally surrounded by clear-cut land, or an oasis within a desert landscape. These studies demonstrated that many of the same principles applied. Human use of resources may also be constrained by the size of the habitat island they occupied. The small mammal diversity found in habitat islands formed by mediaeval city walls, the confines of convent gardens, and collegiate grounds was examined by Armitage (1985). This study was confined to the small mammals that coexisted with people, but a similar approach can be taken with the economic species used by people living in different sized habitat islands. If such habitat islands were small, we might expect to see proportionally greater use of captive and domestic animals. Animal remains identified by zooarchaeologists in sites outside of their present range are usually described as former range extensions. Indeed, this is often most likely, however, human introductions should also be considered as an explanation for the difference in the former range. Our study has shown that human flexibility in the food quest allowed adjustment to changes in faunal diversity found within the West Indian archipelago. We anticipate that similar adjustments were made by people as they colonized other archipelagoes.

ACKNOWLEDGEMENTS

Faunal identifications were made with the support of National Science Foundation Grant BNS 8903377 to ESW, and the identification of materials from the site of En Bas Saline was supported by National Science Foundation Grant BNS 8706697 awarded to K. Deagan. The grants that have made these studies possible are gratefully acknowledged. We also thank the many archeologists who have entrusted the faunal remains to us for study. A number of people identified the remains in these samples and we are indebted to them for their careful work. They include: L. Kozuch, S. de France, S. Scudder, E. Simons, K. Bosworth, and B. Shockey. Our thanks to Sandrine Grouard for translation of the abstract to French and Susan Sandretto for the translation to Spanish. We also thank J. Quinn and T. Schoener for their thoughtful suggestions and review of our manuscript. The order of authorship was determined by flipping a coin.

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APPENDIX 1.—Endemic, introduced, estuarine, reef, and pelagic animals represented in each site designated by the site number listed on Table 1. Quantification is a calculation of minimum numbers of individuals

TAXA	1	2	3	4	5	6	7	8	9	10	11	12	13
ENDEMIC													
Brachyphylla									1	1	9		
Oryzomyine								59	23	53	168	12	14
Brotomys				2									
Isolobodon				4									
Geocapromys		8	1										

APPENDIX 1. (continued)

TAXA	1	2	3	4	5	6	7	8	9	10	11	12	13
Plagiodon					1								
Podicipidae			1										
Puffinus						2					32		2
Procellaridae									1				
Phaethon											2		
Pelecanus													2
Sula		1							7		1		
Ardeidae			1							2			
Phoenicopterus											1		
Aythya												1	
Anatidae				1	1								
Pandion			1										1
Porphyrula												1	
Rallidae			1			2				1			
Laridae	3		1						1		2	1	
Columba					3						1		
Zenaida											5		
Columbidae				1			2	12		16			
Coccyzus	2												
Mimidae								17					
Turdus							1						
Passeriformes				1	2					1			
Trachemys				2	1								
Anolis	3		1		2		3			1			
Cyclura			13	3			3						
Iguana					1				10	14	26		5
Diploglossus				1									
Ameiva					1			1		4	4		
lizard						2							
snake/Alsophis				1	2	3	1	2		1	4		
Bufo					1								
Endemic S	3	2	8	9	10	4	5	5	6	10	12	4	5
Endemic MNI	8	9	20	16	15	9	10	91	43	94	255	15	24
INTRODUCED													
Didelphis													11
Nesophontes							1						
Dasypus													1
Rattus	1												
Dasyprocta									3	9	16		17
Geocapromys	1												
Isolobodon					1	4	3						
Canis			1									4	3
Emydidae									1				
Introduced S	2	0	1	0	1	1	2	0	2	1	1	1	4

APPENDIX 1. (continued)

TAXA	1	2	3	4	5	6	7	8	9	10	11	12	13
Introduced MNI	2	0	1	0	1	4	4	0	4	9	16	4	32
ESTUARINE													
Trichechus				2									
Monachus										3			
Crocodylus		1											
Cheloniidae	1		5	1		2	3	3	4	5	13	9	3
Dasyatis			1										
Rajiformes						2							
Elops				1									
Megalops													3
Elopidae							1						
Albula			47	1		1							2
Anguilla				1	1								
Harengula					43								
Clupeidae	2			4		6	7			6			1
Engraulidae						1							
Strongylura					6		1						
Tylosaurus					3		1				3		
Belonidae		1	3	1		3		4	4	8		4	6
Fundulus							1						
Atherinidae							4						
Centropomus			1	2	1								
Selar	6						1						
Seriola												1	
Gerres				1			2						
Diapterus					4								
Gerreidae			14										
Conodon								1					
Archosargus		1									1		
Calamus		15	2	1		3	5	1			5		
Sparidae	1				1					1			
Bairdiella				3	1	1							
Sciaenops													1
Stellifer													1
Sciaenidae			1										
Mugil				3	7	1							
Clinidae				4		1							
Dormitator							1						
Gobiomorus				1	6		1						
Gobionellus					1								
Trichiurus				1									
Lactophrys		2	2	2					1				
Ostraciidae	1					2							
Estuarine S	5	5	9	16	11	11	12	4	3	5	4	3	7
Estuarine MNI	11	20	76	29	74	23	28	9	9	23	22	14	17

APPENDIX 1. (continued)

TAXA	1	2	3	4	5	6	7	8	9	10	11	12	13
REEF													
Ginglymostoma			1						1			1	
Carcharhinus			1	1	1								1
Carcharhinidae									4				1
Lamniformes	1												
Gymnothorax			1	3					1			1	
Muraenidae						3							
Holocentrus				5	2		4			2	9	1	
Holocentridae	1					17			4				
Scorpaena												2	
Epinephelus		30	10	22	6	15	9	9	17	13	28	10	10
Hypoplectrus						2							
Mycteroperca				3		5					1		1
Serranidae	2												
Malacanthus							1			2			
Caranx	8	4		4	6	18	40		6	4	41	12	4
Chloroscomberus				1									
Selene			1										
Trachinotus				1	1								
Trachurus									2				
Carangidae			5					4					
Lutjanus		8	15		3		33		15		16	2	9
Ocyurus					1	8	4				5		
Lutjanidae				13		18		3		6			
Anisotremus					3		1	3			4	1	
Haemulon		18	17	16	6	20	14	5		14	38	11	2
Orthopristis								1					
Haemulidae									5				
Mulloidichthys						1							
Mullus	121												
Kyphosus								1		1			
Chaetodipterus				1									
Holocanthus				1									
Pomacanthus					1						3		
Abudefduf					1	2					5		
Microspathodon						1				2			
Sphyraena		1	4	4		3				2	8		1
Bodianus				1	3			3	11				
Halichoeres		7	6	9	5	10	11	4	6	4		3	
Lachnolaimus			1	1									
Labridae	1										30		2
Scarus	13	27	19	6	1	9			5	1	98	4	
Sparisoma	20	41	67	30	4	50	20	9	12	19	138	39	8
Acanthurus	7	21	6	11	1	20		1	21	18	82	34	2
Balistes		4		4	4	1	8		3				2

APPENDIX 1. (continued)

TAXA	1	2	3	4	5	6	7	8	9	10	11	12	13
Melichthys		1			3	1			17				
Balistidae	3		5			3				6	37	12	
Sphoeroides			1	2									
Diodon		4	7	2	2		8			2	11	3	1
Diodontidae	1								9				
Reef S	11	12	17	22	19	20	12	11	17	15	17	15	13
Reef MNI	178	166	167	141	54	207	153	43	139	96	554	136	44
PELAGIC													
Cypselurus												1	
Hirundychthys												4	
Exocoetidae	19			13	4	5	17		1				3
Alectis		1											
Scomberomorus					1								
Auxis											7	4	
Euthynnus					3	1						1	
Thunnus					1						15		
Scombridae	9						1	4		12			12
Pelagic S	2	1	0	1	4	2	2	1	1	1	2	4	2
Pelagic MNI	28	1	0	13	9	6	18	4	1	12	22	10	15